Gizzard vs. teeth, it's a tie: food-processing efficiency in herbivorous birds and mammals and implications for dinosaur feeding strategies

Fritz, J ; Hummel, J ; Kienzle, E ; Wings, O ; Streich, W J ; Clauss, Marcus

Abstract: Particle size reduction is a primary means of improving efficiency in herbivores. The mode of food particle size reduction is one of the main differences between herbivorous birds (gizzard) and mammals (teeth). For a quantitative comparison of the efficiency of food comminution, we investigated mean fecal particle sizes (MPS) in 14 herbivorous bird species and compared these with a data set of 111 non-ruminant herbivorous mammal species. In general MPS increased with body mass, but there was no significant difference between birds and mammals, suggesting a comparable efficiency of food processing by gizzards and chewing teeth. The results lead to the intriguing question of why gizzard systems have evolved comparatively rarely among amniote herbivores. Advantages linked to one of the two food comminution systems must, however, be sought in different effects other than size reduction itself. In paleoecological scenarios, the evolution of ''dental batteries,'' for example in ornithopod dinosaurs, should be considered an advantage compared to absence of mastication, but not compared to gizzard-based herbivory.

DOI: https://doi.org/10.1666/10031.1

Gizzard vs. Teeth, it's a tie: food-processing efficiency in herbivorous birds and mammals and implications for dinosaur feeding strategies

Julia Fritz, Jürgen Hummel, Ellen Kienzle, Oliver Wings, W. Jürgen Streich, and Marcus Clauss

Abstract**. —**Particle size reduction is a primary means of improving efficiency in herbivores. The mode of food particle size reduction is one of the main differences between herbivorous birds (gizzard) and mammals (teeth). For a quantitative comparison of the efficiency of food comminution, we investigated mean fecal particle sizes (MPS) in 14 herbivorous bird species and compared these with a data set of 111 non-ruminant herbivorous mammal species. In general MPS increased with body mass, but there was no significant difference between birds and mammals, suggesting a comparable efficiency of food processing by gizzards and chewing teeth. The results lead to the intriguing question of why gizzard systems have evolved comparatively rarely among amniote herbivores. Advantages linked to one of the two food comminution systems must, however, be sought in different effects other than size reduction itself. In paleoecological scenarios, the evolution of "dental batteries," for example in ornithopod dinosaurs, should be considered an advantage compared to absence of mastication, but not compared to gizzard-based herbivory.

Julia Fritz and Ellen Kienzle. Institute of Physiology, Physiological Chemistry and Animal Nutrition, Ludwig-Maximilians-University Munich, Schönleutnerstr. 8, 85764 Oberschleißheim, Germany. E-mail: fritz_julia@yahoo.de

Jürgen Hummel. Institute of Animal Science, Animal Nutrition Group, University of Bonn, Germany

Oliver Wings. Museum of Natural History, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin, Germany

W. Jürgen Streich. Leibniz-Institute of Zoo and Wildlife Research Berlin, Germany

Marcus Clauss.* Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstrasse 260, 8057 Zurich, Switzerland. E-mail: mclauss@vetclinics.uzh.ch

*Corresponding author

Accepted: 24 January 2011

Introduction

Efficient digestion of plant material depends on two main factors, the time ingesta remain within in the gastrointestinal tract (retention time) and the particle size to which the food is processed. The former is important because digestion of hemicellulose and cellulose in plant cell walls by symbiotic microorganisms is a rather slow process (Stevens and Hume 1995) and the latter because smaller particles can be fermented at a faster rate (Cherney et al. 1988; Bjorndal et al. 1990). Moreover, as has recently been demonstrated, retention time in the gut and the efficiency of particle size reduction (i.e., chewing efficiency) may compensate for each other–in large herbivorous mammals, species with relatively lower chewing efficiency have longer digesta retention times (Clauss et al. 2009). The relevance of reducing the particle size of ingested food is well understood (Clauss and Hummel 2005). However, for herbivorous birds, quantitative data on particle size reduction have only been reported sporadically (Moore 1999; Potter et al. 2006). For example, in studies of geese, Moore (1999) stated that the degree to which grass can be degraded by the avian gizzard is comparable to that of chewing by ruminants. However, this statement misses the order of magnitude by which body mass differs between geese and ruminants, as well as the fact that ruminants re-masticate their food during rumination and therefore take an exceptional position within herbivorous mammals (Fritz et al. 2009).

Different strategies have evolved in herbivorous mammals and birds for food processing. Mammals are equipped with a complex dental chewing apparatus, and birds use their muscular stomach (ventriculus or gizzard, which is preceded by the glandular stomach, the proventriculus), functioning as a gastric mill, for mechanical disruption of food (Moore 1999; Mackie 2002). Note that the pyloric part of the stomach of monogastric animals, in particular

mammal carnivores, is also sometimes referred to as a “gastric mill’ where digesta particle size reduction of food of animal origin is achieved by the muscular action of the pylorus (e.g., Barboza et al. 2009: Fig. 5.6). Also note that extant archosaurs such as crocodilians have a stomach anatomy that resembles, with its distinct fundus and pylorus sections, the two-chambered pattern of the avian proventriculus and ventriculus; the pyloric part of the crocodilian stomach is therefore sometimes referred to as “gizzard” (Schwenk and Rubega 2005). The stomach of crocodilians actually contains gastroliths with irregular frequency (Corbet 1960; Cott 1961; Delany and Abercrombie 1986; Platt et al. 2006; Pauwels et al. 2007; Wallace and Leslie 2008), but whether they help reduce ingesta particle size is still debated (Diefenbach 1975; Skoczylas 1978; Schwenk and Rubega 2005; Wings 2007). When compared with the gastrolith mass found in herbivorous birds (~1 % of body mass [Wings and Sander 2007]), the amounts of gastroliths in crocodiles appear rather low (0.1-0.3 % of body mass [Schwenk and Rubega 2005; Pauwels et al. 2007]). In the following text, the words “gastric mill’ and “gizzard’ will be used to denote the ventriculus of birds in which, with the help of gastroliths, the digesta is reduced in particle size.

Birds ingest stones and grit and retain them in the gizzard as gastroliths to enhance the efficiency of mechanical food breakdown (Stevens and Hume 1995; Moore 1998b, Gionfriddo and Best 1999; Mackie 2002; Wings 2007). Several studies revealed that both gastrolith mass (Wings and Sander 2007) and mean grit size (Gionfriddo and Best 1996) are strongly correlated with body mass in herbivorous birds, which might be analogous to different isometric and allometric aspects of the chewing apparatus in herbivorous mammals where measurements such as tooth volume or molar occlusal surface also scale with body mass (Gould 1975; Creighton

1980; Fortelius 1986, 1987; Popowics and Fortelius 1997; Copes and Schwartz 2010). Furthermore, descriptive as well as experimental studies have shown that the muscular mass of the gizzard increases with higher fiber contents in the diet (Pendergast and Boag 1973; Drobney 1984; Herd and Dawson 1984; Piersma et al. 1993; Moore 1998a; Starck 1999; Amerah et al. 2007) and that the amount of grit used is strongly influenced by the type of diet—it increases with increasing coarseness of the diet (Gionfriddo and Best 1996), thus resembling adaptations in muscular or dental design in mammals (Janis 1988; Williams and Kay 2001; Clauss et al. 2008).

The aim of this study was to determine fecal particle sizes of herbivorous birds of different body sizes and to compare these with fecal particle sizes in mammals (Fritz et al. 2009) and reptiles (Fritz et al. 2010). Because fecal particle size is a reliable measure of the effectiveness of reducing food particle size, we wanted to test whether food reduction by muscular grinding is as effective as by chewing with teeth. A potential difference in the efficiency of particle size reduction between gizzards and teeth would be important in comparative considerations of the evolution of herbivory in mammals and birds, or in different dinosaur groups. For example, the evolution of the impressive dental masticatory apparatus of ornithopods, the “dental batteries,” is considered an important factor for the radiation of this clade (Coe et al. 1987; Weishampel and Norman 1989; Wing et al. 1992). In contrast, no radiation of a non-avian dinosaur group has been linked to the evolution of a gastric mill so far. Less efficient particle size reduction by gizzards as compared to teeth could help explain this pattern.

Additionally, we tested in a small, opportunistic sample of individuals the ingesta particle size in the largest extant herbivorous bird, the ostrich (*Struthio camelus*), at the level of the glandular stomach (proventriculus), prior to the effect of the gizzard. Because neither birds (Duke 1997) nor reptiles (Throckmorton 1976; Bjorndal and Bolten 1992; Duke 1997) chew their food, particle sizes of food *ingested* by birds and of feces excreted by reptiles should be similar at similar body size.

Material and Methods

We evaluated the mean fecal particle sizes of captive birds (n = 40; 14 species) from eight zoological institutions in Europe. Fecal particle size is generally regarded as reflecting the ingesta particle size beyond the gizzard. Only adult healthy individuals with no history of diarrhea were sampled. Diets consisted of plant material, mainly grass in their enclosures, hay, vegetables and fruits, and limited amounts of grains/pellets. Because the animals could not be weighed for this study, and weight records usually were not available, body mass was estimated with reference to literature data. The resulting inaccuracy will not be relevant across the large range of body masses investigated in this study, but individual comparisons between pairs of similar-sized species should not be based on this data. Additionally we investigated the contents of the proventriculus and distal colon of six captive, adult *Struthio camelus* from a private ostrich farm in Switzerland. Prior to sampling, animals were kept on grass pasture and maize. All samples were sealed watertight and stored frozen until analysis. Analysis was performed by wet sieving (Retsch® AS 200 digit, Haan, Germany) using nine sieves with mesh sizes of 0.063, 0.125, 0.25, 0.5, 1, 2, 4, 8, and 16 mm (quadrate openings). Sieving time was ten minutes and water throughput 2 l/min. The mean particle size (MPS) was obtained by curve fitting

(TableCurve® 2Dv5.01, Systat Software UK Ltd.) as described by Hummel et al. (2008). An average particle size was calculated for each species or, in the case of ostriches, for each gut segment (Table 1).

Table 1

For comparison with mammals (excluding ruminants) and reptiles, we calculated MPS of the respective data sets the same way (see Appendices 1 and 2). Note that data consisted of the same samples used by Fritz et al. (2009; 2010), measured with the same sieve set as used in the present study. In the former studies MPS had been calculated for 6 sieves (excluding the 0.063, 8, and 16 mm sieves) so a large data set of ruminant species from Clauss et al. (2002), for which only six sieves had been used, could be integrated into the studies. For the bird data, means of percentages of all particles retained on a particular sieve are given in Appendix 3.

Data for birds and non-ruminant mammals were compared using a Generalized Linear Model with body mass as a covariate. Differences in MPS of different gut segments of *S. camelus* were tested by paired *t*-test. All analyses were performed with SPSS® 18.0 (SPSS Inc., Chicago, Illinois, USA). The significance level was set to $p = 0.05$.

Results

There was a highly significant increase of MPS with body mass in the General Linear Model ($p<0.001$), but no difference according to clade ($p=0.410$). No difference was obvious between birds (gastric mill) and mammals (masticating teeth). Mean particle size was 17 times larger in the proventriculus than in the distal colon of *Struthio camelus* (17.33 ± 9.05 mm versus 1.04 ± 0.26 mm, $p < 0.007$) (Fig. 1).

Fig. 1

When dissecting the stomach, we noted obvious differences in texture of glandular stomach content and muscular stomach content (see Fig. 2).

Fig. 2

Discussion

As in herbivorous mammals (Fritz et al. 2009) and reptiles (Fritz et al. 2010), mean fecal particle size increases with body mass in birds. In general, herbivorous birds have fecal particle sizes comparable to those of similarly sized non-ruminant mammals—confirming the assumption of Moore (1999) that mammals and birds achieve similar degrees of particle size reduction in a quantitative way–and, consequently, smaller fecal particle sizes than reptiles achieve (Fritz et al. 2010).

Herbivorous reptiles and birds share the characteristic that they do not masticate their food. According to our expectations, MPS in the proventriculus of ostriches was comparable to fecal particle sizes of herbivorous reptiles (cf. Fig. 1), which reflects the lack of mechanical breakdown of the food at that stage of digestive processing. Without muscular trituration and gastroliths, the degree to which birds could process their food would be comparable to that of reptiles. In contrast to birds, food is not comminuted after ingestion in reptiles, so mouth size and morphology as well as feeding behavior have been considered as factors affecting fecal particle size in reptiles (Bjorndal and Bolten 1992; Fritz et al. 2010). The effect of selective feeding on particle size also has been demonstrated in birds. For example, studies with geese have shown that animals foraged preferentially on smaller food items (Amat 1995; Durant et al. 2009), and that birds may crop food items partially so that the ingested piece is smaller than the whole plant

part. Beak size and morphology are correlated with bite size in birds (Cope et al. 1995a,b; Durant et al. 2003; Van der Graaf et al. 2006), but a potential effect on fecal particle size has not been quantified yet (Durant et al. 2009). Moore (1999) demonstrated that the particle size of the ingested food can affect particle breakdown in the gizzard in geese, but the effect was apparent only when food particle size was already smaller than 2 mm. As diets in the present study comprised only small proportions of pelleted compounds or grains, a relevant systematic effect on the mean fecal particle sizes is unlikely. Nevertheless, the lack of a standardized diet is a limitation of this study. Ideally, the results generated by the comparative method in this study should be evaluated in a controlled experiment where the same roughage is fed to birds and mammals.

It is an interesting question why gastric mills are so rare in the fossil record of terrestrial, non-avian herbivores (Wings 2007; Wings and Sander 2007). Apparently only a few terrestrial herbivorous dinosaurs consistently show evidence of a gastric mill (i.e., gastroliths are consistently associated with skeletal remains); those include the basal ceratopsians *Psittacosaurus* (You and Dodson 2004) and *Yinlong* (Xu et al. 2006), the ornithopod *Gasparinisaura* (Cerda 2008), and derived, nearly toothless theropod dinosaurs from several clades, such as *Limusaurus* (Xu et al. 2009), *Shenzhousaurus* (Ji et al. 2003), *Sinornithomimus* (Kobayashi and Lü 2003), and *Caudipteryx* (Ji et al. 1998; Zhou and Wang 2000). *Psittacosaurus* and *Gasparinisaura* are both equipped with a sophisticated masticatory apparatus in addition to a gizzard with gastroliths (Coria and Salgado 1996; You and Dodson 2004; Sereno et al. 2010); the reason for the evolution of what appears to be a unique double system for food

reduction remains obscure; possibly it is an adaptation for handling exceptionally tough plant food.

Fig. 3

When considering the phylogenetic context of chewing and gizzard systems (Fig. 3; note that in contrast to similar trees in Reilly et al. 2001 and Varricchio 2001, our tree is more restrictive when assigning a gastrolith-containing gizzard system to taxonomic groups), the presence of gizzards in birds, and the putative presence of a gizzard-like pylorus that sometimes contains gastroliths in crocodilians (see "Introduction") could, by phylogenetic bracketing, suggest that the presence of a gizzard with gastroliths and a gastric mill function is a plesiomorphic character in archosaurs (Varricchio 2001). On the other hand, the seeming absence of regular accumulations of gastroliths in articulated skeletal remains of diverse dinosaur and archosaur groups suggests instead that it was the anatomical predisposition—a strong-muscled pyloric stomach part—that was plesiomorphic for archosaurs, and that the development of an actual gastrolith-containing gizzard was an apomorphy that not all groups acquired. Note that even among birds, not all species acquire gastroliths, although their stomach consists of a proventriculus and a ventriculus (Gionfriddo and Best 1999); the variation within and between crocodilian species has already been mentioned. The fact that several different dinosaur lineages evolved a gastrolith-containing gizzard emphasizes that, at least within dinosaurs, the occurrence of gizzards was not constrained by phylogenetic contingency. Additionally, the results of our study suggest that potential reasons for differences in the relative occurrence of a gizzard-gastrolith system and dental mastication cannot be explained by differences in efficiency of particle size reduction, but must be sought in other causes. In the following, we review some of such possible causes.

A gizzard system is evidently advantageous when the overall organismal design demands that the site of particle size reduction be close to the center of gravity; as such, the use of a gizzard is usually linked to the primary characteristic of herbivorous birds, flight. In contrast, adaptations for chewing intrinsically increase the weight of the head. The use of the gizzard system has the potential advantages that intake rate is not limited by chewing (Hummel and Clauss 2011), that no investment in dental tissue is necessary, and that dental wear is not a determinant of senescence as observed in mammals (e.g., Veiberg et al. 2007). The absence of age-dependent tooth wear might even be a contributing factor to the slower onset of senescence in birds as compared to mammals (Western and Ssemakula 1982). On the other hand, the use of a gizzard requires the intake of suitable grit or stones——an action that represents, in the few studies where this has actually been quantified in birds, a relevant proportion of feeding time (Gionfriddo and Best 1999). Additionally, although we think of stones as being ubiquitous, differences in the frequency of gastroliths between crocodile populations have been ascribed to a lack of suitable stones in one particular habitat (Cott 1961; Wallace and Leslie 2008). A masticatory apparatus guarantees independence from the presence of suitable stones.

Another possible factor favoring the evolution of a masticatory apparatus rather than a gizzard in terrestrial herbivores could be space competition in the abdominal cavity, which is particularly relevant in herbivores (Clauss et al. 2003). This might make a gizzard a valuable option only for animals that cannot afford a masticatory apparatus owing to the bauplan requirements for flight, or that are contingency-constrained in the evolution of a masticatory apparatus. If gastrolith mass in general followed the positive allometric scaling observed by

Wings and Sander (2007); i.e., gastrolith mass represents an increasing proportion of body mass with increasing body mass, then this argument might be even more important. Although the allometric increase in gastrolith mass with body mass (according to the equation gastrolith mass in g = 0.001 $BM^{1.20}$, with BM in g) [Wings and Sander 2007] would lead to a gastrolith mass of only 5% of BM at a BM of 30,000 kg—which is still unlikely to pose a serious space problem in the coelomic cavity of sauropods (Franz et al. 2009)—it is striking that gastroliths (in amounts suitable for an avian-style gastric mill) appear to occur mainly in smaller herbivores. It is tempting to speculate that stones more suited for smaller herbivore species are more ubiquitous than those that would be required for very large herbivores. Note that all dinosaurs that are consistently associated with accumulated gastroliths are relatively small, with estimated maximum body masses at or below 20 kg. The maximum body mass of herbivores relying on gastroliths and a gizzard was about 250 kg (moas and elephant birds; Worthy and Holdaway 2002), which is distinctively lower than the maximum sizes achieved by chewing mammals and dinosaurs. Nonetheless, a size limitation due to the gizzard strategy has so far not been demonstrated, in contrast to more concrete indications that mastication may represent a serious limit to maximal body size (Hummel and Clauss 2011). It also remains to be investigated whether particles size reduction in a grinding (gizzard) or mastication (teeth) system differs with respect to energetic efficiency (costs per unit size reduction).

Another factor that might favor a dental apparatus over a gizzard system is an additional function of teeth and mastication apart from ingesta particle size reduction for a more efficient digestion—the oral preparation of food for the final stage of the ingestion process, swallowing. Having particle size reduction take place proximal to the esophagus—and just before swallowing

occurs—may make it possible for an animal to consume a broader spectrum of plant material. It is difficult to fathom how an animal without incisor-like teeth or a parrot-like beak could crop particularly tough food, just as it is difficult to imagine elephants or black rhinoceroses efficiently ingesting large-diameter twigs without the grinding action of large molars. Although empirical data are lacking, we suspect that ingestive mastication facilitates the use of tougher plant material better than a gizzard does in animals of comparable size. A diet containing such particularly tough food might be the reason *Psittacosaurus* and *Gasparinisaura* evolved a grinding dentition in addition to a gizzard. In this respect, it would be helpful to find evidence that chewing and non-chewing dinosaurs systematically use plants in different phenological stages or different plant parts.

In the extant vertebrate fauna, the capacity to reduce particle size is related to the metabolic demands of a species (Reilly et al. 2001; Lucas 2004). Therefore, particle size reduction is often considered the key digestive difference between ecto- and endotherms (Karasov et al. 1986; Farlow 1987; Fritz et al. 2010) that allows endotherms to rely on shorter digesta retention times without losing digestive efficiency (Franz et al. 2011), and hence facilitate the high level of food intake necessary to meet their increased metabolic requirements. Among dinosaurs, differences in the capacity for particle size reduction could thus help to explain potential differences in metabolic levels and growth rates in herbivores—for example, slower-growing stegosaurs (Redelstorff and Sander 2009) and ankylosaurs (Stein and Sander 2009) with no adaptations for particle size reduction versus fast-growing ornithopods (Horner et al. 2000) with their “dental batteries.” In this respect it is particularly relevant that no systematic difference in the size distribution of fecal particles has been found between extant taxa with gizzards and those with chewing teeth, an observation that corresponds to the similarly high

metabolic rates of non-passerine birds and mammals (McNab 2008; 2009) (see Fig. 1). Nonetheless, at least one dinosaur group challenges the simplistic equation of a particle size reduction mechanism with high growth rates–the sauropods.

Not only did sauropod dinosaurs have extremely high growth rates and hence probably a high level of metabolism (Sander et al. 2011), but they also lacked a sophisticated masticatory apparatus (Calvo 1994; Upchurch and Barrett 2000). Therefore, we would automatically suspect that sauropods had a gizzard-gastrolith system for particle size reduction, as has been suggested by many authors (Bakker 1986; Farlow 1987; Weishampel and Norman 1989; Wing et al. 1992; Christiansen 1996; Taggart and Cross 1997; Upchurch and Barrett 2000). Unfortunately, the most recently collated evidence (from a new appraisal of fossil findings and allometric extrapolations [Wings 2004; Wings and Sander 2007]) suggests that sauropods did *not* possess an avian-style gizzard. On the one hand, adult sauropods might actually represent an exceptional example of herbivores that outgrew the body size range where digestive advantages and disadvantages associated with increased body size balance each other (Clauss and Hummel 2005); they thus enter a body size range where advantages due to increasing body size such as enormous relative digestive capacities (Franz et al. 2009) are no longer outbalanced by disadvantages such as large ingesta particle size (because at a certain bite size, food particle size is determined by leaf morphology and cannot increase further [Hummel and Clauss 2011]). On the other hand, the question of how growing sauropods could maintain their high growth rates without efficient reduction in forage particle size still warrants a persuasive answer. A nearly complete, articulated skeleton of an early juvenile sauropod did not contain any gastroliths (Schwarz et al. 2007). Sauropods thus serve as an example that regardless of the relative merits

of gizzards and teeth, other means of achieving high metabolic and growth rates than by systematic particle size reduction must not be discarded.

Acknowledgments

We thank the zoological gardens of Walsrode, Berlin, Munich, Nuremberg, Wuppertal, Zurich, and Basel, and J. Corder for access to samples. This work was supported by DFG grants CL 182/3-1 and CL 182/51 and is contribution number 105 of the DFG Research Unit 533 “The Biology of Sauropod Dinosaurs.” J. Fritz was partly supported by the Karl-Heinz-Kurtze-Foundation. We thank C. Janis, P. Barrett, and one anonymous reviewer for comments that helped improve the original manuscript.

Literature Cited

Amat, J. A. 1995. Effects of wintering greylag geese *Anser anser* on their *Scirpus* food plants. Ecography 18:155-163.

Amerah, A. M., R. G. Lentle, and V. Ravindran. 2007. Influence of feed form on gizzard morphology and particle size spectra of duodenal digesta in broiler chickens. Journal of Poultry Science 44:175-181.

Bakker, R. 1986. The dinosaur heresies. Longman Scientific and Technical, Harlow, U.K.

Barboza, P. S., K. L. Parker, and I. D. Hume. 2009. Integrative wildlife nutrition. Springer, Berlin.

Benton, M. J. 1990. Phylogeny of the major tetrapod groups: morphological data and divergence dates. Journal of Molecular Evolution 30:409-424.

Benton, M. J., and J. M. Clark. 1988. Archosaur phylogeny and the relationships of the Crocodilia. Pp. 295-338 *in* M. J. Benton, ed. The phylogeny and classification of the tetrapods. Systematics Association, Oxford.

Bjorndal, K. A., and A. B. Bolten. 1992. Body size and digestive efficiency in a herbivorous freshwater turtle: advantages of small bite size. Physiological Zoology 65:1028-1039.

Bjorndal, K. A., A. B. Bolten, and J. E. Moore. 1990. Digestive fermentation in herbivores: effect of food particle size. Physiological Zoology 63:710-721.

Brochu, C. A. 2001. Progress and future directions in archosaur phylogenetics. Paleontology 76:1185-1201.

Calvo, J. O. 1994. Jaw mechanics in sauropod dinosaurs. GAIA 10:183-193.

Cerda, I. A. 2008. Gastroliths in an ornithopod dinosaur. Acta Palaeontologica Polonica 53:351-355.

Cherney, J. H., D. J. R. Cherney, and D. R. Mertens. 1988. Fiber composition and digestion kinetics in grass stem internodes as influenced by particle size. Journal of Dairy Science 71:2112-2122.

Christiansen, P. 1996. The evidence for implications of gastroliths in sauropods. GAIA 12:1-7.

Clauss, M., and J. Hummel. 2005. The digestive performance of mammalian herbivores: why big may not be *that* much better. Mammal Review 35:174-187.

Clauss, M., M. Lechner-Doll, and W. J. Streich. 2002. Faecal particle size distribution in captive wild ruminants: an approach to the browser/grazer-dichotomy from the other end. Oecologia 131:343-349.

Clauss, M., R. Frey, B. Kiefer, M. Lechner-Doll, W. Loehlein, C. Polster, G. E. Rössner, and W. J. Streich. 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. Oecologia 136:14-27.

Clauss, M., R. R. Hofmann, W. J. Streich, J. Fickel, and J. Hummel. 2008. Higher masseter mass in grazing than in browsing ruminants. Oecologia 157:377–385.

Clauss, M., C. Nunn, J. Fritz, and J. Hummel. 2009. Evidence for a tradeoff between retention time and chewing efficiency in large mammalian herbivores. Comparative Biochemistry and Physiology A 154:376-382.

Coe, M. J., D. L. Dilcher, J. O. Farlow, D. M. Jarzen, and D. A. Russell. 1987. Dinosaurs and land plants. Pp. 225-258 *in* E. M. Friis, W. G. Chaloner, and R. Crane, eds. The origins of angiosperms and their biological consequences. Cambridge University Press, Cambridge.

Cope, D. R., M. J. J. E. Loonen, J. M. Rowcliffe, and R. A. Pettifor. 1995a. Larger barnacle geese (*Branta leucopsis*) are more efficient feeders: a possible mechanism for observed body size-fitness relationships. Journal of Zoology 265:37-42.

———. 1995b. Larger barnacle geese (*Branta leucopsis*) are more efficient feeders: a possible mechanism for observed body size-fitness relationships. Journal of Zoology 265:37-42.

Copes, L. E., and G. T. Schwartz. 2010. The scale of it all: postcanine tooth size, the taxon-level effect, and the universality of Gould's scaling law. Paleobiology 36:188-203.

Corbet, P. S. 1960. The food of a sample of crocodiles (*Crocodilus niloticus*) from Lake Victoria. Proceedings of the Zoological Society of London 133:561-572.

Coria, R. A., and J. O. Calvo. 2002. A new iguanodontian ornithopod from Neuquen Basin, Patagonia, Argentina. Journal of Vertebrate Paleontology 22:503–509.

Coria, R. A., and L. Salgado. 1996. A basal iguanodontian (Ornithischia: Ornithopoda) from the Late Cretaceous of South America. Journal of Vertebrate Paleontology 16:445-457.

Cott, H. B. 1961. Scientific results of an enquiry into the ecology and economic status of the Nile crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. Transactions of the Zoological Society of London 29:211-356.

Creighton, G. K. 1980. Static allometry of mammalian teeth and the correlation of tooth size and body size in contemporary mammals. Journal of Zoology 191:435-443.

Delany, M. F., and C. L. Abercrombie. 1986. American alligator food habits in northcentral Florida. Journal of Wildlife Management 50:348-353.

Diefenbach, C. O. 1975. Gastric function in *Caiman crocodilus*. 1. Rate of gastric digestion and gastric motility as a function of temperature. Comparative Biochemistry and Physiology A 51:259-265.

Drobney, R. 1984. Effect of diet on visceral morphology of breeding wood ducks. Auk 101:93-98.

Duke, G. E. 1997. Gastrointestinal physiology and nutrition in wild birds. Proceedings of the Nutrition Society 56:1049-1056.

Durant, D., H. Fritz, S. Blais, and P. Duncan. 2003. The functional response in three species of herbivorous Anatidae: effects of sward height, body mass and bill size. Journal of Animal Ecology 72:220-231.

Durant, D., L. Desnouches, H. Fritz, M. Guillemain, and F. Mesléard. 2009. Size-related consumption of *Scirpus maritimus* tubers by greylag geese *Anser anser* explained by their functional response. Behavioural Processes 80:39-45.

Farlow, J. O. 1987. Speculations about the diet and digestive physiology of herbivorous dinosaurs. Paleobiology 13:60-72.

Fortelius, M. 1986. Isometric scaling of mammalian cheek teeth is also true metabolic scaling. Pp. *in* D. E. Russell, J.-P. Santoro, and D. Sigogneau-Russell, eds. Teeth revisited. Proceedings of the VIIth International Symposium on Dental Morphology. Mémoires du Museum National d'Histoire Naturelle C 53:459-462.

———. 1987. A note on the scaling of dental wear. Evolutionary Theory 8:73-75.

Franz, R., J. Hummel, E. Kienzle, P. Kölle, H. C. Gunga, and M. Clauss. 2009. Allometry of visceral organs in living amniotes and its implications for sauropod dinosaurs. Proceedings of the Royal Society B 276:1731-1736.

Franz, R., J. Hummel, D. W. H. Müller, M. Bauert, J.-M. Hatt, and M. Clauss. 2011. Herbivorous reptiles and body mass: effects on food intake, digesta retention,

digestibility and gut capacity, and a comparison with mammals. Comparative Biochemistry and Physiology A 158:94-101.

Fritz, J., J. Hummel, E. Kienzle, C. Arnold, C. Nunn, and M. Clauss. 2009. Comparative chewing efficiency in mammalian herbivores. Oikos 118:1623-1632.

Fritz, J., J. Hummel, E. Kienzle, W. J. Streich, and M. Clauss. 2010. To chew or not to chew: faecal particle size in herbivorous reptiles and mammals. Journal of Experimental Zoology A 313:579-586.

Gauthier, J. 1986. Saurischian monophyly and the origin of birds. *In* K. Padian, ed. The origin of birds and the evolution of flight. California Academy of Sciences Memoir 8:1-55. San Francisco.

Gionfriddo, J. P., and L. B. Best. 1996. Grit-use patterns in North American birds: the influence of diet, body size, and gender. Wilson Bulletin 108:658-696.

———. 1999. Grit use by birds—a review. Current Ornithology 15:89-148.

Gould, S. J. 1975. On the scaling of tooth size in mammals. American Zoologist 15:351-362.

Herd, R., and T. Dawson. 1984. Fibre digestion in the emu, *Dromaius novaehollandiae*, a large bird with a simple gut and high rates of passage. Physiological Zoology 57:70-84.

Horner, J. R., A. de Ricqlès, and K. Padian. 2000. Long bone histology of the hadrosaurid dinosaur *Maiasaura peeblesorum*: growth dynamics and physiology based on an ontogenetic series of skeletal elements. Journal of Vertebrate Paleontology 20:115-129.

Hummel, J., J. Fritz, E. Kienzle, E. P. Medici, S. Lang, W. Zimmermann, W. J. Streich, and M. Clauss. 2008. Differences in fecal particle size between free-ranging and captive individuals of two browser species. Zoo Biology 27:70-77.

Hummel, J., and M. Clauss. 2011. Feeding and digestive physiology. *In* N. Klein, K. Remes, C. T. Gee, and M. Sander, eds. Understanding the life of giants. The biology of the sauropod dinosaurs. Indiana University Press, Bloomington (in press).

Janis, C. M. 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals and the correlation of these factors with dietary preferences. *In* D. E. Russell, J.-P. Santoro, and D. Sigogneau-Russell, eds. Teeth revisited. Proceedings of the VIIth International Symposium on Dental Morphology. Mémoires du Muséum National d'Histoire Naturelle C 53:367-387.

Ji, Q., P. J. Currie, M. A. Norell, and S. A. Ji. 1998. Two feathered dinosaurs from northeastern China. Nature 393:753-761.

Ji, Q., M. A. Norell, P. J. Makovicky, K. Q. Gao, S. A. Ji, and C. Yuan. 2003. An early ostrich dinosaur and implications for ornithomimosaur phylogeny. American Museum Novitates 3420:1-19.

Karasov, W. H., E. Petrossian, L. Rosenberg, and J. M. Diamond. 1986. How do food passage rate and assimilation differ between herbivorous lizards and nonruminant mammals? Journal of Comparative Physiology B 156:599-609.

Kobayashi, Y., and J. C. Lü. 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. Acta Palaeontologica Polonica 48:235-259.

Lucas, P. W. 2004. Dental functional morphology: how teeth work. Cambridge University Press, Cambridge.

Mackie, R. 2002. Mutualistic fermentative digestion in the gastrointestinal tract: diversity and evolution. Integrative and Comparative Biology 42:319-326.

McNab, B. K. 2008. An analysis of the factors that influence the level and scaling of mammalian BMR. Comparative Biochemistry and Physiology A 151:5-28.

———. 2009. Ecological factors affect the level and scaling of avian BMR. Comparative Biochemistry and Physiology A 152:22-45.

Moore, S. J. 1998a. The comparative functional gizzard morphology of several species of birds. Australian Journal of Zoology 46:359-368.

———. 1998b. Use of an artificial gizzard to investigate the effect of grit on the breakdown of grass. Journal of Zoology 246:119-124.

———. 1999. Food breakdown in an avian herbivore: who needs teeth? Australian Journal of Zoology 47:625-632.

Pauwels, O. S. G., B. Barr, M. L. Sanchez, and M. Burger. 2007. Diet records for the dwarf crocodile (*Osteolaemus tetraspis tetraspis*) in Rabi Oil Fields and Loango National Park, Southwestern Gabon. Hamadryad 31:258-264.

Pendergast, B., and D. Boag. 1973. Seasonal changes in the internal anatomy of spruce grouse in Alberta. Auk 90:307-317.

Piersma, T., A. Koolhaas, and A. Dekinga.1993. Interactions between stomach structure and diet choice in shorebirds. Auk 110:552-564.

Platt, S. G., T. R. Rainwater, A. G. Finger, J. B. Thorbjarnarson, T. A. Anderson, and S. T. McMurry. 2006. Food habits, ontogenetic dietary partitioning and observations of foraging behaviour of Morelet's crocodile (*Crocodylus moreletti*) in northern Belize. Herpetological Journal 16:281-290.

Popowics, T. E., and M. Fortelius. 1997. On the cutting edge: tooth blade sharpness in herbivorous and faunivorous mammals. Annales Zoologici Fennici 34:73-88.

Potter, M. A., R. G. Lentle, C. J. Minson, M. J. Birtles, D. Thomas, and W. H. Hendriks. 2006. Gastrointestinal tract of the brown kiwi (*Apteryx mantelli*). Journal of Zoology 270:429-436.

Redelstorff, R., and P. M. Sander. 2009. Long and girdle bone histology of Stegosaurus: implications for growth and life history. Journal of Vertebrate Paleontology 29:1087-1099.

Reilly, S. M., L. D. McBrayer, and T. D. White. 2001. Prey processing in amniotes: biomechanical and behavioral patterns of food reduction. Comparative Biochemistry and Physiology A 128:397-415.

Sander, P. M., A. Christian, M. Clauss, R. Fechner, C. T. Gee, E. M. Griebeler, H. C. Gunga, J. Hummel, H. Mallison, S. F. Perry, H. Preuschoft, O. W. M. Rauhut, K. Remes, T. Tütken, O. Wings, and U. Witzel. 2011. Biology of the sauropod dinosaurs: the evolution of gigantism. Biological Reviews 86:117-155.

Schwarz, D., T. Ikejiri, B. H. Breithaupt, P. M. Sander, and N. Klein. 2007. A nearly complete skeleton of an early juvenile diplodocid (Dinosauria: Sauropoda) from the Lower Morrison Formation (Late Jurassic) of north central Wyoming and its implications for early ontogeny and pneumaticity in sauropods. Historical Biology 19:225-253.

Schwenk, K., and M. Rubega. 2005. Diversity of vertebrate feeding systems. Pp. 1-41 *in* J. M. Starck and T. Wang, eds. Physiological and ecological adaptations to feeding in vertebrates. Science Publishers, Enfield, N.H.

Sereno, P. C., Z. Xijin, and T. Lin. 2010. A new psittacosaur from Inner Mongolia and the parrot-like structure and function of the psittacosaur skull. Proceedings of the Royal Society of London B 277:199-209.

Skoczylas, R. 1978. Physiology of the digestive tract. Pp. 589-717 *in* C. Gans, and K. A. Gans, eds. Biology of the Reptilia. Academic Press, London.

Starck, J. M. 1999. Phenotypic flexibility of the avian gizzard: rapid, reversible and repeated changes of organ size in response to changes in dietary fibre content. Journal of Experimental Biology 202:775-785.

Stein, M., and M. Sander. 2009. Long bone histology and growth patterns in ankylosaurs. Journal of Vertebrate Paleontology 29:185A.

Stevens, C. E., and I. D. Hume. 1995. Comparative physiology of the vertebrate digestive system. Cambridge University Press, Cambridge.

Taggart, R. E., and A. T. Cross. 1997. The relationship between land plant diversity and productivity and patterns of dinosaur herbivory. Pp. 403-416 *in* D. L. Wolberg, E. Stump, and G. Rosenberg, eds. Dinofest International: proceedings of a symposium held at Arizona State University. National Academy of Natural Sciences, Philadelphia.

Throckmorton, G. S. 1976. Oral food processing in two herbivorous lizards, *Iguana iguana* (Iguanidae) and *Uromastix aegypticus* (Agamidae). Journal of Morphology 148:363-390.

Upchurch, P., and P. M. Barrett. 2000. The evolution of sauropod feeding mechanisms. Pp. 79-122 *in* H. D. Sues, ed. Evolution of herbivory in terrestrial vertebrates: perspectives from the fossil record. Cambridge University Press, Cambridge.

Van der Graaf, A. J., P. Coehoorn, and J. Stahl. 2006. Sward height and bite size affect the functional response of barnacle geese *Branta leucopsis*. Journal of Ornithology 147:479-484.

Varricchio, D. J. 2001. Gut contents from a cretaceous tyrannosaurid: implications for theropod dinosaur digestive tracts. Journal of Paleontology 75:401-406.

Veiberg, V., A. Mysterud, J. M. Gaillard, D. Delorme, G. Van Laere, and F. Klein. 2007. Bigger teeth for longer life? Longevity and molar height in two roe deer populations. Biology Letters 3:268-270.

Wallace, K. M., and A. J. Leslie. 2008. Diet of the Nile crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. Journal of Herpetology 42:361-368.

Weishampel, D. B., and D. B. Norman. 1989. Vertebrate herbivory in the Mesozoic; jaws, plants, and evolutionary metrics. *In* J. O. Farlow, ed. Paleobiology of the dinosaurs. Geological Society of America Special Paper 238:87-100.

Western, D., and J. Ssemakula. 1982. Life history patterns in birds and mammals and their evolutionary interpretation. Oecologia 54:281-290.

Williams, S. H., and R. F. Kay. 2001. A comparative test of adaptive explanations for hypsodonty in ungulates and rodents. Journal of Mammalian Evolution 8:207-229.

Wing, S. L., H. D. Sues, B. H. Tiffney, R. K. Stucky, D. B. Weishampel, R. A. Spicer, D. Jablonski, C. E. Badgley, M. V. H. Wilson, and W. L. Kovach. 1992. Mesozoic and early Cenozoic terrestrial ecosystems. Pp. 327-416 *in* A. K. Behrensmeyer, J. D. Damuth, W. A. DiMichele, R. Potts, H. D. Sues, and S. L. Wing, eds. Terrestrial ecosystems through time: evolutionary paleoecology of plants and animals. University of Chicago Press, Chicago.

Wings, O. 2004. Identification, distribution, and function of gastroliths in dinosaurs and extant birds with emphasis on ostriches (*Struthio camelus*). Dissertation thesis, University of Bonn, Germany.

———. 2007. A review of gastrolith function with implications for fossil vertebrates and a revised classification. Acta Palaeontologica Polonica 52:1-16.

Wings, O., and P. M. Sander. 2007. No gastric mill in sauropod dinosaurs: new evidence from analysis of gastrolith mass and function in ostriches. Proceedings of the Royal Society of London B 274:635-640.

Worthy, T. H., and R. N. Holdaway. 2002. The lost world of the moa: prehistoric life of New Zealand. Indiana University Press, Bloomington.

Xu, X., C. Forster, J. Clark, and J. Mo. 2006. A basal ceratopsian with transitional features from the Late Jurassic of northwestern China. Proceedings of the Royal Society B 273:2135-2140.

Xu, X., J. M. Clark, J. Mo, J. Choiniere, C. A. Forster, G. M. Erickson, D. W. E. Hone, C. Sullivan, D. A. Eberth, S. Nesbitt, Q. Zhao, R. Hernandez, C. K. Jia, F. I. Han, and Y. Guo. 2009. A Jurassic ceratosaur from China helps clarify avian digital homologies. Nature 459:940-944.

You, H. L., and P. Dodson. 2004. Basal Ceratopsia. Pp. 478–493 *in* D. B. Weishampel, P. Dodson, and H. Osmólska, eds. The Dinosauria. University of California Press, Berkeley.

Zhou, Z.-H., and X.-L. Wang. 2000. A new species of *Caudipteryx* from the Yixian Formation of Liaoning, northeast China. Vertebrata PalAsiatica 38:111-127.

FIGURE 1. Mean fecal particle size (average value per species) in non-ruminant herbivorous mammals, herbivorous reptiles and herbivorous birds (data from Table 1, data for mammals and reptiles see Appendices 1 and 2) across the body size range; average mean particle size in proventriculus of *Struthio camelus*

FIGURE 2. Dissected stomach of an ostrich (*Struthio camelus*) and contents of different stomach parts. Note differences in content textures. In contrast to the proventriculus, strong muscles surround the gizzard that contains the gastroliths and plant matter that has been ground. Oes, esophagus; Prov, proventriculus; Gizz, gizzard; SI, small intestine. Scale in cm.

FIGURE 3. Phylogenetic relationships of tetrapods with grinding molars and gastrolith-using gastric mills. Note that several large clades (without dental batteries and gastric mills) are omitted for reasons of clarity (based on Gauthier 1986; Benton and Clark 1988; Benton 1990; Ji et al. 1998; Brochu 2001; Coria and Calvo 2002; Ji et al. 2003; Kobayashi and Lü 2003; Xu et al. 2006; Xu et al. 2009). For a discussion of a gastric mill in Crocodilomorpha, see the text.

TABLE 1. Body mass (BM) and mean fecal particle size (MPS) in birds used in this study. *n* = number of fecal samples analyzed.

Species	*n*	BM* ± SD kg		MPS ± SD mm	
Struthio camelus					
Proventriculus	6	100.0	-	17.330	9.051
Distal colon	6	100.0	-	1.042	0.259
Feces	8	97.50	± 7.071	0.876	± 0.378
Rhea americana	5	20.00	-	1.399	± 0.701
Casuarius casuarius	2	60.00	-	2.486	± 2.110
Dromaius novaehollandiae	4	40.00	-	2.039	± 1.668
Dendrocygna viduata	1	0.65	-	0.397	-
Philacte canagica	3	2.50	-	0.498	± 0.120
Chen caerulescens	3	3.00	-	0.579	± 0.112
Eulabeia indica	1	2.50	-	0.342	-
Rufibrenta ruficollis	3	1.50	-	0.452	± 0.018
Branta leucopsis	4	1.53	± 0.050	0.420	± 0.256
Branta sandvicensis	1	2.00	-	0.435	-
Chauna torquata	2	3.75	± 0.354	0.404	± 0.183
Catreus wallichii	1	1.30	-	0.150	-
Tragopan satyra	2	1.70	± 0.566	0.575	± 0.069

Appendix 1

Body mass (BM; weighted, estimated or taken from literature) in kg and mean fecal particle size (MPS) in mm ± standard deviation (SD) respectively in non-ruminating mammals (* = foregut fermenter, other species are hindgut fermenters); *n* = number of fecal samples analyzed (gs = group sample pooled from a group of animals).

Species			*n*	BM ± SD		MPS ± SD	
				kg		mm	
Monodelphis domestica	Didelphimorphia	Didelphidae	2 (gs)	0.100	-	0.331	± 0.184
Phascolarctus cinereus	Diprodontia	Phascolarctidae	5	6.188	± 1.128	0.293	± 0.047
Vombatus ursinus	Diprodontia	Macropodidae	3	40.000	-	0.432	± 0.072
*Bettongia penicillata**	Diprodontia	Macropodidae	2 (gs)	1.250	± 0.354	0.492	± 0.518
*Dendrolagus matschiei**	Diprodontia	Macropodidae	3	13.000	-	0.881	± 0.409
*Macropus agiles**	Diprodontia	Macropodidae	2	15.000	-	0.630	± 0.106
*Macropus fuliginosus**	Diprodontia	Macropodidae	1	50.000	-	0.888	-
*Macropus giganteus**	Diprodontia	Macropodidae	3	60.000	± 25.000	0.572	± 0.436
*Macropus parma**	Diprodontia	Macropodidae	2 (gs)	6.000	-	0.283	± 0.088
*Macropus rufogriseus **	Diprodontia	Macropodidae	3	16.500	± 0.866	0.831	± 0.087
*Macropus rufus**	Diprodontia	Macropodidae	2	62.500	± 31.820	1.441	± 0.302
*Wallabia bicolor**	Diprodontia	Macropodidae	2	15.000	-	0.646	± 0.211
Hapalemur griseus	Primates	Lemuridae	1	1.200	-	1.608	-
Lemur catta	Primates	Lemuridae	3	3.333	± 0.289	2.246	± 0.773
Varecia variegata	Primates	Lemuridae	4	4.000	-	2.387	± 1.247
Alouatta palliata	Primates	Cebidae	1	7.000	-	3.190	-
Lagothrix lagotricha	Primates	Cebidae	2	7.500	± 4.243	2.333	± 1.861
Pithecia pithecia	Primates	Cebidae	2	1.800	± 0.283	0.381	± 0.068
Cercopithecus pygerythrus	Primates	Cercopithecidae	1	5.500	-	0.527	-
Macaca sylvanus	Primates	Cercopithecidae	1	24.000	-	0.688	-
Mandrillus sphinx	Primates	Cercopithecidae	2	27.500	± 0.707	1.249	± 0.374
*Presbytis obscurus**	Primates	Cercopithecidae	1	7.000	-	0.706	-
*Presbytis entellus**	Primates	Cercopithecidae	2 (gs)	20.000	± 1.414	0.848	± 0.179
*Presbytis cristata**	Primates	Cercopithecidae	3 (gs)	13.167	± 2.021	0.762	± 0.173
*Pygathrix nemaeus**	Primates	Cercopithecidae	5	9.000	± 1.414	0.598	± 0.103
Theropithecus gelada	Primates	Cercopithecidae	6	17.500	-	2.221	± 0.757
Hylobates lar	Primates	Hylobatidae	2	5.500	-	2.545	± 0.055
Hylobates lar moloch	Primates	Hylobatidae	2	5.500	± 0.707	1.122	± 0.012
Hylobates syndactylus	Primates	Hylobatidae	4	12.500	± 1.683	4.786	± 4.041
Gorilla gorilla	Primates	Pongidae	8	97.563	± 55.537	3.896	± 1.941
Pan paniscus	Primates	Pongidae	5	39.120	± 9.366	3.207	± 0.761
Pan troglodytes	Primates	Pongidae	5	52.220	± 26.187	1.942	± 0.938
Pongo pygmaeus	Primates	Pongidae	5	60.000	± 37.495	2.142	± 1.305

*Choloepus didactylus**	Xenarthra	Megalonychidae	5	10.000	± 1.414	0.419	± 0.119
Lepus europaeus	Lagomorpha	Leporidae	5	4.500	-	0.346	± 0.083
Cynomys ludovicianus	Lagomorpha	Leporidae	1 (gs)	1.150	-	0.673	-
Oryctolagus cuniculus	Rodentia	Sciuridae	5	4.000	-	0.379	± 0.040
Marmota bobac	Rodentia	Sciuridae	1	5.000	-	0.197	-
Marmota marmota	Rodentia	Sciuridae	1	5.000	-	0.950	-
Sciurus carolinensis	Rodentia	Sciuridae	1	0.450	-	0.271	-
Sciurus variegatoides	Rodentia	Sciuridae	1	0.550	-	0.319	-
Xerus inauris	Rodentia	Sciuridae	1 (gs)	0.750	-	0.568	-
Castor canadensis	Rodentia	Castoridae	2	30.000	-	2.517	± 0.437
Castor fiber	Rodentia	Castoridae	3	30.000	-	3.121	± 1.094
Pedetes capensis	Rodentia	Pedetidae	1 (gs)	3.500	-	0.211	-
Jaculus jaculus	Rodentia	Dipodidae	1 (gs)	0.055	-	0.247	-
Acomys russatus	Rodentia	Muridae	2 (gs)	0.045	-	0.396	± 0.070
Lemniscomys barbarus	Rodentia	Muridae	1 (gs)	0.040	-	0.318	-
Mastomys natalensis	Rodentia	Muridae	1 (gs)	0.065	-	0.417	-
Micromys minutus	Rodentia	Muridae	2 (gs)	0.006	-	0.213	± 0.014
Mus musculus	Rodentia	Muridae	1	0.020	-	0.231	-
Cricetomys emini	Rodentia	Cricetidae	1 (gs)	1.250	-	0.413	-
Cricetulus griseus	Rodentia	Cricetidae	1 (gs)	0.040	-	0.323	-
Gerbillus perpallidus	Rodentia	Cricetidae	2 (gs)	0.040	-	0.293	± 0.011
Graphiurus murinus	Rodentia	Cricetidae	1 (gs)	0.025	-	0.436	-
Hypogeomys antimena	Rodentia	Cricetidae	2	1.350	-	0.508	± 0.207
Microtus brandti	Rodentia	Cricetidae	1 (gs)	0.045	-	0.136	-
Microtus fortis	Rodentia	Cricetidae	1 (gs)	0.045	-	0.149	-
Phodopus roborovskii	Rodentia	Cricetidae	2 (gs)	0.030	-	0.299	± 0.045
Phodopus sungorus	Rodentia	Cricetidae	3 (gs)	0.040	-	0.287	-
Seketamys calurus	Rodentia	Cricetidae	1 (gs)	0.060	-	0.406	-
Ctenodactyles gundi	Rodentia	Ctenodactylidae	1	0.250	-	0.235	-
Atherurus africanus	Rodentia	Hystricidae	1 (gs)	1.750	-	0.303	-
Hystrix africaeaustralis	Rodentia	Hystricidae	1 (gs)	20.000	-	1.560	-
Hystrix cristata	Rodentia	Hystricidae	5 (gs)	20.000	-	1.908	± 0.726
Hystrix indica	Rodentia	Hystricidae	2 (gs)	20.000	-	1.110	± 0.199
Petromus typicus	Rodentia	Petromuridae	1	0.200	-	0.281	-
Heterocephalus glaber	Rodentia	Bathyergidae	2 (gs)	0.052	-	0.531	± 0.053
Chinchilla chinchilla	Rodentia	Chinchillidae	3 (gs)	0.550	± 0.050	0.154	± 0.068
Lagostomus maximus	Rodentia	Chinchillidae	5	4.130	± 0.790	0.176	± 0.012
Cavia aperea	Rodentia	Caviidae	3 (gs)	0.625	-	0.109	± 0.026
Cavia aperea f. *porcellus*	Rodentia	Caviidae	6 (gs)	0.783	± 0.075	0.172	± 0.158
Dolichotis patagonum	Rodentia	Caviidae	5 (gs)	7.500	± 0.354	0.273	± 0.060
Galea musteloides	Rodentia	Caviidae	1 (gs)	0.450	-	0.104	-

Kerodon rupestris	Rodentia	Caviidae	1	0.750	-	0.160	-
Hydrochaerus hydrochaeris	Rodentia	Hydrochaeridae	3	40.000	-	0.401	± 0.084
Dasyprocta azarae	Rodentia	Dasyproctidae	1 (gs)	3.000	-	0.697	-
Dasyprocta leporina	Rodentia	Dasyproctidae	2 (gs)	3.250	-	0.544	± 0.432
Octodon degus	Rodentia	Octondontidae	2 (gs)	0.230	-	0.168	± 0.008
Spalacopus cyanus	Rodentia	Octondontidae	1	0.090	-	0.235	-
Capromys pilorides	Rodentia	Capromyidae	3	5.000	± 0.500	0.118	± 0.024
Myocastor coypus	Rodentia	Myocastoridae	5 (gs)	7.600	± 0.894	0.762	± 0.245
Procavia capensis	Hyracoidae	Procaviidae	2 (gs)	3.075	± 0.106	1.177	± 0.856
Elephas maximus	Proboscidae	Elephantidae	18	3183.672	± 821.540	7.086	± 4.192
Loxodonta africana	Proboscidae	Elephantidae	12	2733.333	± 1053.206	6.177	± 1.725
Trichecus manatus	Sirenia	Trichechidae	4	850.000	± 57.735	5.113	± 1.990
Equus africanus f. asinus	Perissodactyla	Equidae	11	216.364	± 0.545	1.096	± 0.545
Equus africanus somalicus	Perissodactyla	Equidae	4	268.750	23.936	1.479	± 0.509
Equus grevyi	Perissodactyla	Equidae	5	342.000	± 10.954	1.652	± 0.800
Equus hemionus kiang	Perissodactyla	Equidae	6	245.000	5.477	0.516	± 0.090
Equus hemionus kulan	Perissodactyla	Equidae	5	250.000	-	0.779	± 0.207
Equus hemionus onager	Perissodactyla	Equidae	2	250.000	-	0.900	± 0.024
Equus przewalskii	Perissodactyla	Equidae	5	292.000	± 40.866	0.533	± 0.070
Equus przewalskii f. caballus	Perissodactyla	Equidae	37	460.000	± 223.709	1.224	± 0.537
Equus quagga antiquorum	Perissodactyla	Equidae	3	216.667	± 28.868	1.378	± 0.551
Equus quagga boehmi	Perissodactyla	Equidae	6	275.000	± 27.386	2.153	± 1.069
Equus quagga burchelli	Perissodactyla	Equidae	2	215.000	± 21.213	1.309	± 0.005
Equus quagga chapmani	Perissodactyla	Equidae	5	290.000	± 22.361	1.441	± 0.918
Equus zebra hartmannae	Perissodactyla	Equidae	5	314.000	± 21.909	1.335	± 0.499
Ceratotherium simun	Perissodactyla	Rhinocerotidae	8	1938.750	± 370.769	9.782	± 3.003
Diceros bicornis	Perissodactyla	Rhinocerotidae	12	985.000	± 200.839	9.276	± 3.348
Rhinocerus unicornis	Perissodactyla	Rhinocerotidae	6	2150.000	± 151.658	4.161	± 1.239
Tapirus indicus	Perissodactyla	Tapiridae	5	275.000	± 17.678	3.555	± 1.261
Tapirus terrestris	Perissodactyla	Tapiridae	10	195.500	± 17.552	2.887	± 1.064
Ailuropoda melanoleuca	Carnivora	Ailuridae	8	98.750	± 9.910	8.267	± 4.296
Ailurus fulgens	Carnivora	Ailuridae	5 (gs)	5.000	-	1.084	± 0.343
*Babyrousa babyrussa**	Cetartiodactyla	Suidae	3	60.000	-	3.082	± 1.172
Phacochoerus aethiopicus	Cetartiodactyla	Suidae	5	85.000	-	2.182	± 0.242
Tayassu tajacu	Cetartiodactyla	Tayassuidae	5	23.000	-	0.567	± 0.083
*Hippopotamus amphibius**	Cetartiodactyla	Hippopotamidae	6	2333.333	± 302.765	13.758	± 6.578
*Choeropsis liberiensis**	Cetartiodactyla	Hippopotamidae	4	250.000	-	7.163	± 2.035

Note that the MPS was calculated on the basis of a sieve analysis with nine sieves (in contrast to the data presented in Fritz et al. 2009).

Appendix 2

Body mass (BM) and mean fecal particle size (MPS) in herbivorous reptiles. *n* = number of fecal samples analyzed.

Species	*n*	BM ± SD		MPS ± SD	
		kg		mm	
Iguana iguana	8	2.711	± 0.432	8.025	± 8.172
Cyclura cornuta	5	4.500*	± 1.118	10.614	± 14.781
Corucia zebrata	10	0.423	± 0.123	10.128	± 4.024
Dipsochelys dussumieri	6	102.500*	± 86.125	23.712	± 10.087
Testudo gigantea	5	158.000*	± 31.937	26.247	± 3.814
Geochelone nigra	7	104.286*	± 21.492	16.170	± 6.605
Testudo radiata	3	10.000*	-	8.187	± 1.515
Testudo pardalis	4	30.000*	-	19.161	± 14.068
Testudo sulcata	3	90.000*	-	9.921	± 8.196
Testudo horsfieldii	1	1.200	-	7.114	-
Testudo hermanni	14	0.808	± 0.464	5.103	± 3.726
Testudo graeca	13	1.545	± 0.884	6.755	± 5.911

Note that the MPS was calculated on the basis of a sieve analysis with nine sieves (in contrast to the data presented in Fritz et al. 2009).

Appendix 3

Percentage (dry mass) (± SD) of all particles retained on a particular sieve (linear pore size) in birds used in this study.

Species	*n*	0.063 mm	0.125 mm	0.25 mm	0.5 mm	1 mm	2 mm	4 mm	8 mm	16 mm
Struthio camelus										
Proventriculus	6	3.498 ± 2.825	3.331 ± 2.043	4.601 ± 3.268	5.591 ± 3.369	7.409 ± 3.491	16.302 ± 4.817	12.145 ± 6.727	11.886 ± 5.356	35.236 ± 21.462
Distal colon	6	18.431 ± 2.903	16.413 ± 3.536	18.518 ± 2.246	16.751 ± 3.995	15.560 ± 4.006	10.433 ± 2.812	2.923 ± 2.374	0.970 ± 1.199	0.000 ± 0.000
Feces	8	19.554 ± 3.230	20.756 ± 8.941	19.677 ± 3.088	15.701 ± 3.954	12.737 ± 6.232	8.556 ± 4.219	2.291 ± 2.325	0.727 ± 1.109	0.000 ± 0.000
Rhea americana	5	9.561 ± 4.566	25.839 ± 10.266	25.451 ± 7.568	15.311 ± 4.921	7.045 ± 4.398	9.813 ± 14.881	3.179 ± 4.861	0.989 ± 0.960	2.811 ± 2.342
Casuarius casuarius	2	5.352 ± 0.832	17.270 ± 5.526	22.618 ± 16.638	16.203 ± 7.629	11.293 ± 8.924	9.515 ± 6.199	6.592 ± 2.705	9.301 ± 10.096	1.856 ± 1.036
Dromaius novaehollandiae	4	11.746 ± 7.534	22.583 ± 19.320	13.848 ± 6.127	13.421 ± 9.683	9.330 ± 2.092	14.155 ± 6.833	12.769 ± 16.924	2.141 ± 3.490	0.007 ± 0.013
Dendrocygna viduata	1	15.584 -	24.299 -	27.106 -	19.942 -	13.069 -	0.000 -	0.000 -	0.000 -	0.000 -
Philacte canagica	3	9.047 ± 3.428	19.145 ± 4.910	30.167 ± 1.164	27.784 ± 10.699	12.097 ± 6.947	1.580 ± 2.224	0.181 ± 0.313	0.000 -	0.000 -
Chen caerulescens	3	9.825 ± 2.167	19.023 ± 5.755	25.087 ± 3.470	30.526 ± 6.747	11.727 ± 3.757	3.104 ± 0.421	0.708 ± 0.606	0.000 -	0.000 -
Eulabeia indica	1	7.899 -	25.000 -	37.437 -	26.881 -	2.784 -	0.000 -	0.000 -	0.000 -	0.000 -
Rufibrenta ruficollis	3	9.960 ± 0.157	25.323 ± 1.275	30.142 ± 6.278	24.862 ± 6.055	8.384 ± 0.393	0.938 ± 1.062	0.313 ± 0.310	0.078 ± 0.110	0.000 -
Branta leucopsis	4	14.901 ± 4.035	33.702 ± 8.864	29.897 ± 2.883	13.390 ± 3.985	4.736 ± 2.942	2.477 ± 3.851	0.897 ± 1.583	0.000 -	0.000 -
Branta sandvicensis	1	7.441 -	20.508 -	30.743 -	30.962 -	9.765 -	0.581 -	0.000 -	0.000 -	0.000 -
Chauna torquata	2	15.613 ± 4.053	22.820 ± 11.565	32.808 ± 1.979	18.309 ± 3.486	7.582 ± 7.076	2.867 ± 3.077	0.000 -	0.000 -	0.000 -
Catreus wallichii	1	39.221 -	34.129 -	24.942 -	1.393 -	0.000 -	0.183 -	0.133 -	0.000 -	0.000 -
Tragopan satyra	2	15.550 ± 3.876	24.434 ± 0.970	28.150 ± 2.478	18.708 ± 5.649	9.620 ± 0.130	1.817 ± 1.178	0.596 ± 0.842	1.125 ± 0.216	0.000 -